

Spawning, Development and Ecology of Some Higher Neogastropoda from the Caribbean Sea of Colombia (South America)

BY

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(17 Text figures)

INTRODUCTION

THE EGG CAPSULES of the members of the superfamilies Volutacea, Mitracea and Conacea from the Caribbean Coast of Colombia show little variety of shapes even though secreted by species of such different taxonomic affinities. Within the family Olividae (*Oliva reticularis* Lamarck, 1810, *Olivella perplexa* Olsson, 1956) Mitridae (*Vexillum puella* (Reeve, 1845)), Volutidae (*Voluta virescens* [Lightfoot, 1786]), Marginellidae (*Hyalina avena* (Kiener, 1834)), Terebridae (*Terebra cinerea* (Born, 1778)) and Turridae (*Drillia solida* C. B. Adams, 1830, *Crasispira* sp.) cupola-shaped egg capsules are formed and in the family Conidae and the genus *Conus* bilaterally flattened, asymmetrical, vasiform capsules are produced. This fits rather well into the picture demonstrated by other authors regarding the egg capsules of most of these superfamilies (D'ASARO, 1970; EDWARDS, 1968; KNUDSEN, 1950; KOHN, 1961; LAMY, 1928; LEBOUR, 1945; MARCUS & MARCUS, 1959; OSTERGAARD, 1955; PAINE, 1962; PERRY & SCHWENGEL, 1955; PONDER, 1972; THORSON, 1946).

The spawn of 13 species of higher Neogastropoda from Santa Marta (Colombia) is described, 10 of them here for the first time. Additional material was collected in the summer of 1971 on Curaçao (Netherlands Antilles).

This study was supported by the Deutsche Forschungsgemeinschaft, which made possible a stay of 18 months at the Instituto Colombo Aleman (ICAL) in Santa Marta, Colombia and a 10 day visit to the Caraibisch Marien Biologisch Instituut (Carmabi) in Curaçao.

Identification of the egg-laying females was accomplished with the help of publications by WARMKE & AB-

BOTT, 1961 and KAUFMANN & GÖTTING, 1970. Dr. R. Tucker Abbott checked and corrected the determinations on material mailed to him.

The shells of the veligers or crawling young hatching from most of the here described types of capsules are figured and described by BANDEL (1975c).

METHODS

Spawn was collected in the sea near the ICAL mainly with the help of fins, mask and snorkel and only in rare cases by aqualung diving. The egg cases of *Voluta virescens* and *Conus largillierti* Kiener, 1848 were obtained from material dredged with fishing nets by Rudo von Cosel and by myself.

Animals and spawn were collected from fall 1970 to spring 1972. Most egg cases described herein were produced by animals held in aquaria with seawater running 12 hours a day. In one case (*Conus jaspideus pygmaeus* Reeve, 1844) the manner of capsule production could be observed in detail on the glass and plastic walls of the aquaria.

Freshly spawned egg-masses were marked or taken out of the aquaria and then observed in glass dishes filled with seawater that was renewed every 2 days. The capsules were drawn by my wife with the help of a binocular microscope immediately after spawning. Capsular dimensions were determined on fresh oothecae containing living embryos, if possible. The spawn was observed in the laboratory of ICAL at a room temperature of 25 to 27°C until the young hatched. The time of development in the

glass dishes was more or less the same as that in aquaria and in the sea.

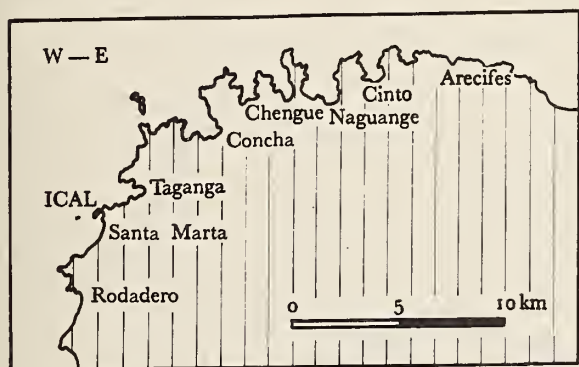


Figure 1

Map of the coast line near Santa Marta, Colombia, showing the collecting stations for the individuals mentioned in this report

Remarks on the Ecology of the Adult Individuals:

Oliva reticularis Lamarck, 1810 is a habitant of sandy bottoms and was found all around Santa Marta in depths of water from $\frac{1}{2}$ m to over 20m. In areas with muddy dark sands, as for example in the bay of Santa Marta, shell coloration is olive-green, while in pure quartz-sands, as for example near the beach of the bay of Villa Concha, and in the pure white carbonaceous sand of the Ensenada Chengue, shell coloration is light reddish brown.

Similar light reddish brown coloration was noted on animals found at the Lac, a large, shallow, open lagoon on the island of Bonaire (Netherlands Antilles).

Oliva reticularis usually is buried shallowly within the sand and only the long, very agile siphon is extended over the surface. Food, as for example burrowing *Bivalvia*, worms and remains of fish thrown from the fishermen's boats, is spotted by the siphon and reached subsurface while shallowly burrowing through the sand. The animal leaves a clearly visible trail on the surface of the sediment, revealing where it had moved within the bottom. If the food lies on top of the substrate, the carnivore will leave the sand 5 - 10cm in front of its prey, will take hold of it as soon as it reaches it, and will retreat into the substrate immediately afterwards. In the aquarium with a sandy bottom substrate this food uptake could be observed very well. When fresh fish meat is thrown into the aquarium, *Oliva* individuals approaching under the surface usually within a short time (minutes) will emerge from the sand and reach the meat in an almost direct approach.

After testing the prey with the siphon it takes hold of the flesh, envelops it with its large posterior foot and within less than a minute it will burrow into the sand again. First contact with the meat, wrapping it into the foot and disappearing into the sediment to complete disappearance was often accomplished within 15 seconds. While locomotion on and within the sand can be quite rapid, steep walls like those of the aquaria and rock faces can not be negotiated by *Oliva*.

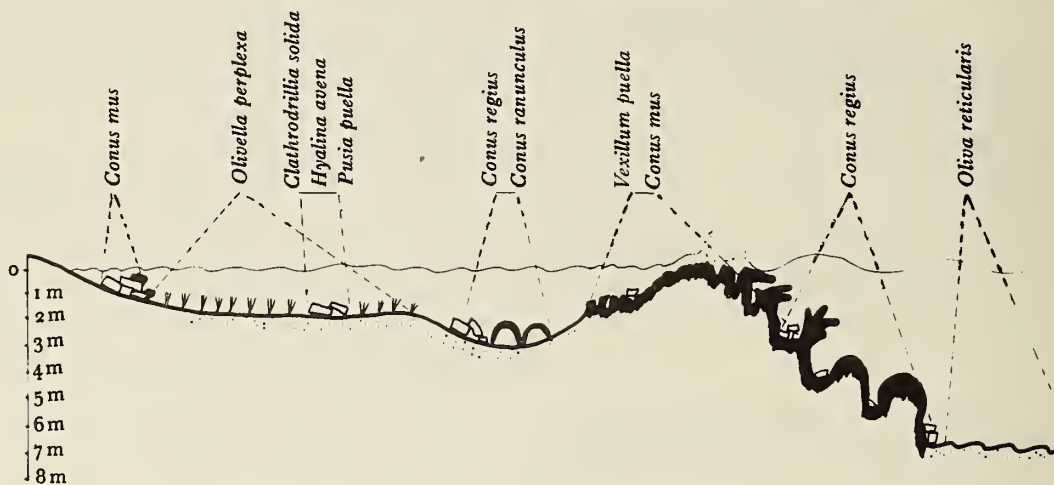
Olivella perplexa Olsson, 1956 lives within muddy sediment everywhere around Santa Marta from about 1 m of depth downwards. Living individuals and dead shells may be found in all sieve probes of a few handfuls of sediment. An especially flourishing population of this species was encountered in the muddy sediment of the northern extension of the bay of Chengue. Here the bottom water is influenced by very warm ($30 - 33^{\circ}\text{C}$) and saline (and therefore heavier) lagoonal water derived from a shallow lagoon behind a beach bar that is connected to the bay by a narrow canal. Each handful of surface sediment here contained more than 20 living individuals of the scavenging and carnivorous species. In the aquarium *O. perplexa* requires a muddy bottom substrate, or it will climb up the aquarium walls and leave the water, drying out within a short time. Individuals of this species are found in thickets of all sorts of filamentous, minute algae growing on rocks or larger boulders below the zone of direct wave action, as well as in soft sediments.

Vexillum puella (Reeve, 1845) occurs under rocks and in crevices in cliffs and large boulders in depths between $\frac{1}{2}$ and 2 m. Its occurrence lies in all rocky environments encountered around Santa Marta from rubble beaches to cliff debris and coral reef rubble. Individuals may also be obtained on the exposed surfaces of rocks and cliffs which here are overgrown with a heavy cover of calcareous algae. In aquaria individuals of this species can be fed easily with fish meat.

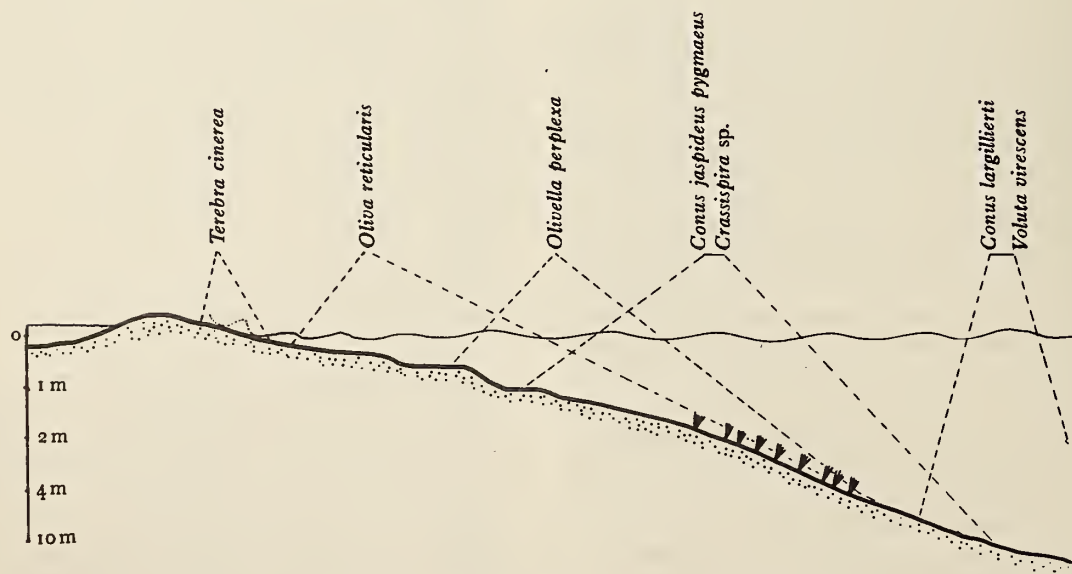
Voluta virescens [Lightfoot, 1786] prefers sandy and muddy bottoms as its environment where it usually can be found buried within the sediment. To change its locality it has to come up to the surface of the substrate and crawl to a new location. In aquaria, *Voluta* usually remains hidden in the sediment during daylight and will leave its resting place in darkness and move about on the sediment and climb up the smooth aquarium walls. Individuals of this species probably live on annelid worms which are hidden in the sediment. Most commonly, living animals were found washed up on the beach from Santa Marta Rodadero after strong wave action due to storms in the open Caribbean Sea. Living animals were also dredged in considerable numbers off-shore from the airport of Santa Marta in depths of 6 - 12 m on muddy substrate. All these

Figure 2

Generalized profiles demonstrating typical habitats of the species the spawn of which is described:



A. from left to right: rocky shore; shallow lagoon bottom with turtle grass and single, loose rocks; depression behind the reef with large, hollow, single coral colonies; coral reef; and rippled sand at its seaward base



B. from left to right: sand beach with water leaking through it from a pool, formed by a fresh water creek; rippled sand; turtle grass on pure sand, later muddy sand; and silty to muddy bottom

individuals carried sea anemones, 2 - 4 cm long, attached to the shell opposite the aperture. When transferred to an aquarium, it showed that the volutes, used as a hard base for attachment by the coelenterates, bury themselves at a depth that the polyps of the coelenterate could reach the surface while feeding and could quickly retract into the sediment if disturbed.

Hyalina avena (Kiener, 1834) was found regularly under rocks and in coral reef rubble in 60 cm to 2 m depths. The small gastropod is also encountered in the thickets of algal growth covering rocks and boulders at these depths. The individuals of this species live on mollusks, such as minute gastropods and bivalves, which, quite similar as in *Oliva reticularis*, are enveloped by the posterior part of the foot before being eaten. With small bivalves *Hyalina avena* can be successfully fed in the aquarium and can be held in quite small spaces if seawater can pass freely through them.

Conus mus Hwass, 1792 settles within the tidal range on all rocky cliffs and boulder-strewn beaches with surf action of different strength. It is not found in depths below 2 m. Some exposure to air is tolerated, but individuals of this species are usually hidden in wet, sun-protected crevices if the environment becomes dry during low tides. On cliffs with strong surf, *C. mus* avoids open rock surfaces and remains hidden in protected crevices and the depressions carved out by sea urchins. Here they hunt for annelids. Individuals can climb from protruding rock projections on their own mucus down through free water to new holdfasts.

Conus regius Gmelin, 1791 is restricted in its occurrence to coral reefs or similar reef structures, as, for example, the beach rock bar protecting the lagoon of the bay of Arecifes. In both reefs the undersides of rocks and living and dead corals in the shelter of the breakwater are the preferred habitats. In the bay of Chengue and the bay of Cinto, individuals occupy the large cavities under semi-spherical coral colonies occurring in 2 - 3 m deep water directly behind the reef and just in front of the lagoonal sea-grass bottom. Here the animals may be found mostly half buried in the sand forming the base of these cavities; they seem to attach themselves to the roof of the hollow only when secreting egg-capsules. The same type of habitat is preferred by individuals of this species found close to the Carmabi on Curaçao. It is probable that *C. regius* feeds on annelids although it was never observed feeding even though maintained over long periods of time in the aquaria.

Conus jaspideus pygmaeus Reeve, 1844 is the most common species of the genus found in the area of Santa

Marta. All muddy and sandy bottoms from 0 to 30 m of depth are inhabited by individuals of this species, often in rich populations. Only shifting bottoms with much current action are avoided. The occurrence extends somewhat into warm and saline waters as found, for example, in the lagoon of the bay of Chengue. Brackish water is avoided. *Conus jaspideus pygmaeus* usually remains hidden in the sediment during sunny daylight, but will search for food when clouds cover the sky, at dawn, and at night. Their food consists of annelids. Locomotion in this species is rather rapid in comparison with the other members of the genus *Conus* mentioned here. Individuals living in mud differ from those living in sand by possessing a thick, light brown periostracum hiding the grey shell with purplish dots. When in search for food, the animals crawl on the broad foot on the surface of the sediment. If an animal wants to hide it dips into the sediment by quick, strong forward motions and is buried within 5 to 10 seconds.

Conus largillierti Kiener, 1848 was only rarely found on sand in depths below 6 m, in the bay of Santa Marta. Individuals of this species can be dredged more regularly from muddy bottoms in deeper water (10 - 12 m) off the airport of Santa Marta. Rudo von Cosel found *C. largillierti* in the Gulf of Uraba in a depth of 50 m. Even though the animals were kept in aquaria for months, nothing can be reported about their feeding habits. It seems probable that they will also feed on annelids.

Conus ermineus Born, 1778 lives in a large variety of environments, but is quite rare everywhere. Few individuals were collected on sandy bottom in the bay of Santa Marta in water deeper than 6 m. Others were found together with *C. regius* under corals and large coral fragments behind the coral reefs in the bays of Chengue and Cinto in depths of about 2 m. On Curaçao individuals may be encountered hidden under living and dead corals within the coral zone in depths of 2 to 30 m. Usually they are found half-buried in sand in the shelter of a cavity and only capsule-secreting females along with copulating males were seen on the undersides of living and dead corals. It may be that individuals of this large species feed on fish, but this could not be observed in the aquarium where individuals were kept for months.

Terebra cinerea (Born, 1778) is restricted in its occurrence to a very specialized environment in the area of Santa Marta. Representatives of this species were found buried in sand within the splash zone to $\frac{1}{2}$ m below it. But only such parts of the beach were inhabited where fresh or brackish water, originating in ponds behind the beach, would penetrate. These ponds are fed by creeks or small rivers. *Terebra cinerea* uses the surf to change its location

on the beach. It comes to the surface of the sand and is here picked up by the surf. The animals thus washed up by a wave take hold with their oval to round, flat, spade-like foot in the sand at the point where the wave starts to recede. This quick anchoring by the propodium is sufficiently strong to hold the animal at this locality, while its shell is turned, pointing upward or downward the slope of the beach with each coming or going wave. Usually 1 or 2 waves are resisted in this way, then the animal has pulled itself into the sediment in a vertical position. It moves into the sand until the tip of the apex disappears. Inside the sand the animal continues its locomotion until it has found a position parallel with the surface of the substrate. Near Santa Marta, a large population is found in the bay of Nague. Here, at the southern end of this large bay, a creek coming from the mountains and flowing all year, sinks through the beach sand. This beach is only settled by *T. cinerea* where this creek ends and further south where a brackish water creek sinks through it. Between both localities the sand is composed of particles of the same grainsize and the beach shows the same surf conditions but is not inhabited by individuals of this species. At the bay of Villa Concha another, much smaller population is found at the southern end of the beach where brackish water is pooled up behind it. A maximum density of about 10 animals per square meter of beach surface is encountered at the Nague. MARCUS & MARCUS (1959) described *T. cinerea* in detail and have found remains of an annelid in its intestines. Food, therefore, must consist of annelids which inhabit the beachsand in especially dense populations where outflowing fresh water provides nourishment in abundance.

Drillia solida C. B. Adams, 1830 lives on and mostly under rocks below the ICAL and among coral rubble in the Chengue bay in depths of $\frac{1}{2}$ to 2 m. Individuals of this species were kept in the aquarium for a long time, but they were never observed feeding. According to their feces, which are usually organic and only shed at long time intervals (BANDEL, 1974b) they must feed on soft animal prey, but are not attracted by fresh fish meat.

Crassispira sp. is found in silty and sandy bottoms from just below turbulent water down to over 15m depth, all around Santa Marta. Especially rich populations were encountered just offshore of the beach of the bay of Taganga where subsurface groundwater comes up and additional food to all sorts of scavengers is provided by fishermen of this village. *Crassispira* most probably lives on worms inhabiting muddy and sandy substrates. The snail is mostly hidden within the substrate.

DESCRIPTION

Oliva reticularis Lamarck, 1810

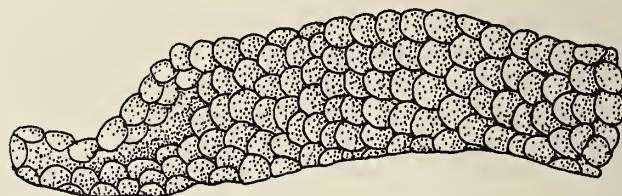
Figures 3A 3B, 3C

Two egg masses of *Oliva reticularis* were found in June, 1971 in aquaria where well fed animals were held for some time.

An egg mass has the shape of a hollow tube, 4 cm long and 1.3 cm in diameter, the walls consisting of about 200 flat, scale-like capsules with their escape apertures point-

Figure 3

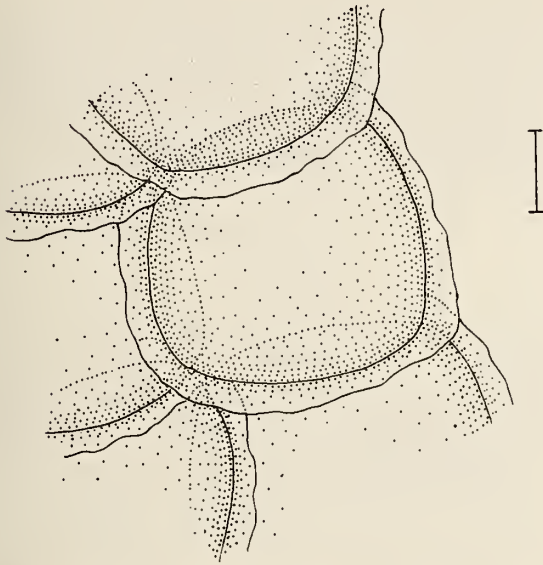
Egg mass of *Oliva reticularis*



A. general view of the whole egg capsule tube (scale = 1 cm)



B. single capsule seen from the inside of the tube (scale = 1 mm)



C. single capsule seen from the outside of the tube (scale = 1 mm)

ing toward the inside of the tube. One end of the tube is closed and there the oldest capsules, secreted first, are located. The ones near the open end, therefore, were secreted last. The tube is half-buried in the sand, with the internal lumen unfilled.

A single capsule shows a completely smooth outside which corresponds to the curvature of the whole tube, is consequently slightly convex. Toward the inside of the egg mass the capsule wall is slightly concave and carries an oval escape aperture in its center; this is surrounded by a thickened ridge. The membrane of the escape aperture is transparent, colorless, and delicately striped like the section of an onion. The long axis of the membrane is accompanied by a suture that continues across the capsule sides which are covered by a fine net of wrinkles similar to a fingerprint. The flat capsule is surrounded on its narrow sides by a rim, which is used at one side of the egg mass as attachment to an older capsule. This is done in such a way that the younger capsule is attached with its rim from the inside to the rim of the older capsule. Thus the scaly appearance of the egg mass is produced. Seen from the outside, the older capsules overlap the younger. The rim is transparent and colorless, while the capsule walls are slightly opaque. One capsule is about 4 mm wide and 3½ mm long, and of minute height. The long axis is parallel

to the long axis of the egg mass tube. Embryos are yellowish white at first, change to brownish yellow to light brown and hatch as red-brown veligers. All eggs develop into veligers, the shell of which is sculptured. Each capsule contains 150 - 200 embryos.

Olivella perplexa Olsson, 1956

(Figure 4)

Egg-capsules produced by *Olivella perplexa* were found in great numbers attached to the shells of other living prosobranchs (mostly *Conus jaspideus pygmaeus*) in the muddy sediment of the northern extension of the bay of Chengue. Up to 7 capsules of different ages were found on single shells.

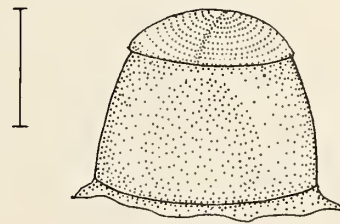


Figure 4

Egg capsule of *Olivella perplexa* seen from above
(scale = 1 mm)

The egg capsule consists of a transparent, colorless hemisphere, broadest at the base. It is affixed to the substrate by a round basal membrane extending only into a small rim beyond the capsule walls. The cupola is differentiated into a lower part with smooth walls, and an upper cover sculptured with delicate concentric striae. Both parts are separated from each other by a sharp groove. In addition, the capsule is differentiated into 2 equal halves by a vertical suture which is clearly visible only on the upper cupola. The one white egg develops in more than 8 days into a crawling young resembling the adult in its shape. Before it can hatch from the 1½ mm wide and almost as high capsule, the whole upper cupola is thrown off. It does not dissolve as a whole but only the narrow rim of it, situated in the groove separating upper and lower part of the capsule, dissolves.

Vexillum puella (Reeve, 1845)

(Figure 5)

The spawn of *Vexillum puella* was found only in aquaria, produced by individuals held in captivity. Due to their small size they might easily have been overlooked in the sea, but were produced all year round in the aquarium. The female requires about 30 minutes for the secretion of one capsule. After the round, soft capsule has passed down the foot in a fold and has been sucked into the capsule gland, a motion of the capsule fluid is noted for a few minutes, after which the soft "egg-drop" remains invisible until the gland has loosened itself from it, revealing a hardened and durable capsule in its final shape.

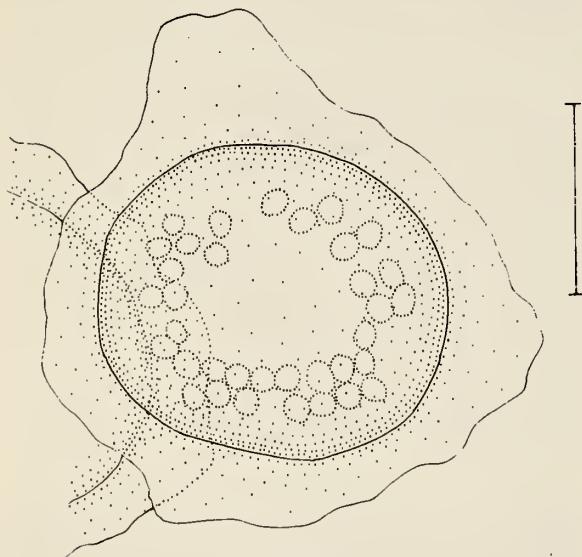


Figure 5

Egg capsule of *Vexillum puella* seen from above
(scale = 1 mm)

The capsules were affixed to the walls of the aquarium and to the leaves of *Sargassum* in irregular groups or singly.

Each capsule is cupola-shaped and consists of an outer smooth wall ending on the basal membrane which extends in an irregular rim beyond this outer wall. Inside, held by this cupola, lies a lens-shaped body containing 25-28 embryos. The outer cupola is transparent and colorless, the inner lens-shaped cover has a slightly opaque wall. In dimension, the oothecae are 2mm wide, about 1.2mm high, and have a round outline. The embryos are white at the

beginning and are arranged in a ring, leaving some open space near the rim and in the center. Later in development the embryos change color to brown because of the color of the developing shell. After 8 to 10 days of development an escape aperture appears in the central part of the cupola. Its oval shape was not visible earlier.

Voluta virescens [Lightfoot, 1786]

(Figure 6)

Egg capsules of *Voluta virescens* were dredged on the 14th of October, 1971 from the muddy bottom offshore from the airport at Santa Marta in depths of from 10 to 12m. On the 8th of August, 1971, Rudo von Cosel found eggcases south of Punta Broqueles.

The capsules were attached to dead shells of bivalves or to the spawn ribbons of *Melongena melongena* (see BANDEL, in press). Each capsule is attached singly, but up to 6 capsules of about the same stage of development could be found on one *Melongena* eggmass. Here the flat capsule sides of this buccinacean spawn are used for attachment. On a single clam shell up to 2 capsules of *Voluta* were found.

Each ootheca is a shallow cupola with a round shape in outline, attached to the substrate by a clear, colorless, smooth, basal membrane extending only as a narrow rim beyond the walls. The walls are smooth and transparent except for a fine-grained, slightly opaque structure. The escape aperture is situated in an eccentric position; it is surrounded by a ridge and closed by a membrane that is more opaque than the remaining capsule. This membrane

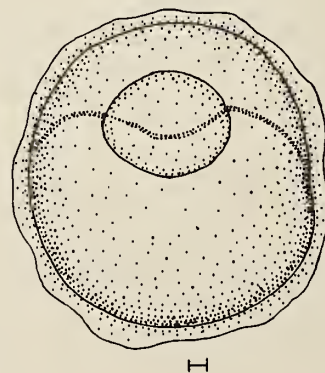


Figure 6

Egg capsule of *Voluta virescens* seen from above
(scale = 1 mm)

is divided into 2 unequal halves by a curving suture which continues along the capsule sides to the rim of the basal membrane as a thickened ridge. Each capsule measures about 1 cm in diameter and 3 mm in height. At the beginning of their development about 200 eggs are concentrated in an irregular rod in the center of the capsule interior. Only 1 or 2 embryos will develop and devour all other eggs during their development. After 38 days the young hatch as miniature adult-like snails.

Hyalina avena (Kiener, 1834)

(Figure 7)

Capsules produced by *Hyalina avena* could only be found attached to bivalve shells in the aquarium. Due to their small size they are easily overlooked in the open sea.

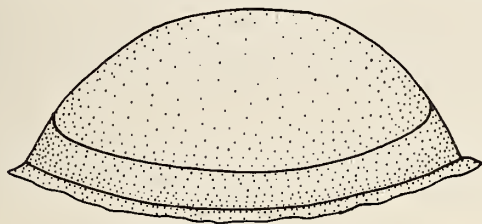


Figure 7

Egg capsule of *Hyalina avena* seen from the side
(scale = 1 mm)

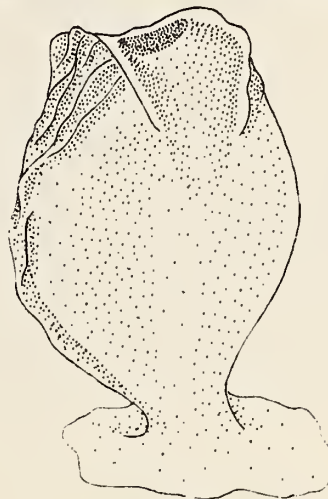
The cupola-shaped capsule has an oval outline; it is attached to the substrate by a basal membrane which does not extend over the capsule walls. The cupola is divided into 2 parts which are separated from each other by a thickened line in the lower part of the cupola. A weak, sinuated suture divides the capsule vertically into 2 halves. The capsule wall shows an internal granulation and a smooth surface.

About 5 embryos take up only little of the intracapsular space at the beginning of their development, but later fill the entire interior. When they are ready to hatch, the whole lid of the capsule falls off along the line near the basal walls of the cupola. Crawling young with a whitish shell finally leave the 1.3 mm long and 1.0 mm wide capsule which is about $\frac{1}{2}$ mm high.

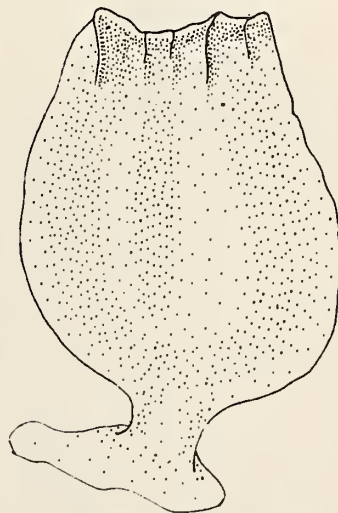
Conus mus Hwass, 1792

(Figures 8A, 8B)

Spawn was observed in the sea at $\frac{1}{2}$ to 1 m depth, fixed to the underside of rocks below the ICAL and in waters shallower than $\frac{1}{2}$ m fixed to large coral fragments in la-



A. seen with its concave side



B. seen with its convex side

Figure 8

Egg capsule of *Conus mus*
(scale = 1 mm)

goons protected by coral reefs or coral patch growths in the bay of Chengue. East and west of the Carmabi Institute on Curaçao spawn of this species can be found in large numbers on the underside of rubble in tide pools and shallow water.

Animals did not spawn in captivity.

The capsules of an egg mass are arranged in the pattern of a row, convex side of one capsule following the concave side of its neighbor. Up to 17 capsules are secreted by one female. Usually a number of females spawn at the same time in the same locality. Each capsule is attached to the substrate by a firm, broad basal membrane.

Neighboring basal membranes of capsules arranged in rows overlap each other at their rims, thus forming a common base of attachment for each spawn mass. Each flattened, tongue-shaped, opaque white capsule has a somewhat vertically convex upper side and an almost smooth concave lower side. Its apical plate is tilted toward the lower side and bordered by 2 wing-like folds carrying a ridge each. The ridges continue into the thickened, lamel-

lar rims surrounding the narrow, oval escape aperture. A thin, transparent membrane closes the escape aperture. Two sutures extend from the narrow ends of the escape aperture down both narrow sides toward the basal membrane. Each suture is accompanied by small wrinkles in the basal part of the capsule. In the upper part 3-5 lateral ridges follow it, ending in the wing-like folds. Each capsule stands on a solid peduncle somewhat displaced laterally. It contains 500-700 embryos which hatch as small veligers after 8-12 days of development. A capsule is up to 7 mm high, at the base 5 and at the top $2\frac{1}{2}$ mm wide, and $\frac{1}{2}$ mm thick. The colorless veliger carries a sculptured shell.

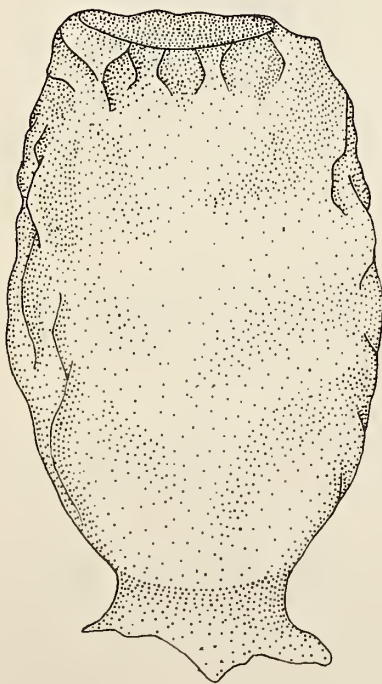
Conus regius Gmelin, 1791

(Figure 9A, 9B)

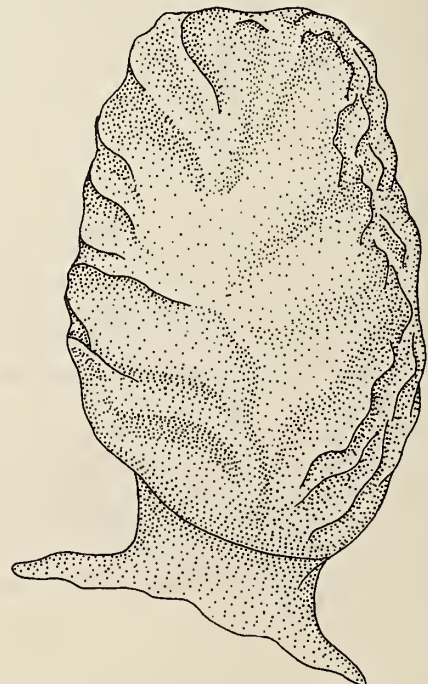
Spawning females were found between June and August 1971 under flat *Acropora* fragments and hollow hemi-

Figure 9

Egg capsule of *Conus regius*
(scale = 1 mm)



A. seen with its concave side



B. seen with its convex side

spherical coral colonies behind the southern coral reef of the bay of Chengue. In July 1971, spawning females were found in similar environments close to the Carmabi on Curaçao.

The spawn consists of rows of capsules. These count 4 to 10 capsules and 4 to 10 rows constitute one egg mass exhibiting the same pattern, one beside the other. Thus, each female secretes up to 42 capsules. Often a few females (up to 5 were observed) were found spawning simultaneously at the same locality. In a row, the concave capsule side is followed by the convex side of its neighbor and thus all escape apertures within one spawn mass point in the same direction. The shape of the capsules corresponds in most details to that described for individuals found in Florida (D'ASARO, 1970). The flattened, roughly rectangular, opaque white capsules are wrinkled unevenly on all sides, somewhat more so on the convex side. The peduncle is displaced laterally. The escape aperture is closed by a transparent membrane and covers the entire apical region. Capsules are 11 mm high, 7 mm wide and 1½ mm thick, which means that they are smaller than those described by D'Asaro from Florida. All 100 to 200 eggs, which are white at first, develop and hatch after 10 days as transparent, colorless veligers with sculptured shells.

Conus jaspideus pygmaeus Reeve, 1844

(Figures 10A, 10B)

Spawn of *Conus jaspideus pygmaeus* could be found throughout the year on empty bivalve shells and other hard substrates on soft bottoms in the sea around Santa Marta.

Animals held in the aquarium produced spawn in great quantities. Often up to 7 females secreted capsules at the same time to the walls of an aquarium, 5 of them constructing one common egg mass. Each female produces an egg mass consisting of about 15 capsules. It was possible to observe the spawning activities in detail. The drop-like, soft capsule containing the eggs appears on the side of the foot bordering the mantle cavity. It is moved forward on the epithelium of the foot, either well visible on the surface or invisible in a fold continuous to the capsule gland. This gland is situated in the central part of the anterior foot sole. The soft egg capsule is sucked into the capsule gland and moved up and down inside it for 2 to 4 minutes. This motion becomes increasingly slower. After 6 to 17 minutes the gland is removed from the now hardened capsule which has assumed its final shape. A new soft capsule drop is passed down from the mantle cavity after the foot has moved to a new spot about 6 minutes after the previous capsule has been finished.

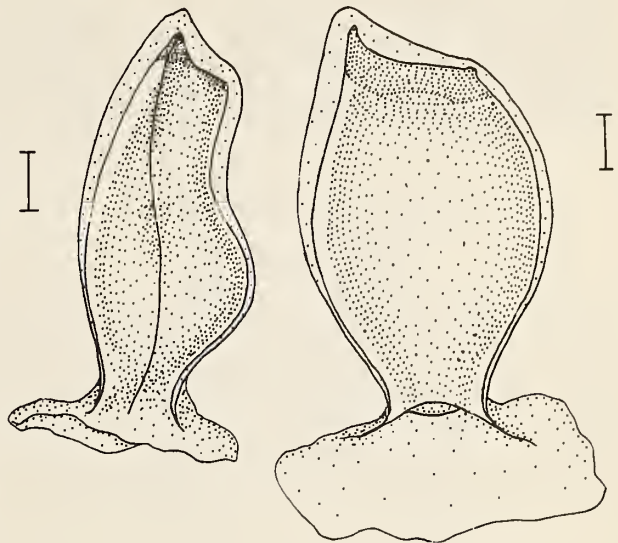


Figure 10

Egg capsule of *Conus jaspideus pygmaeus*

A. seen with its narrow side

B. seen with its broad side

(scale = 1 mm)

Little orientation of the egg capsules in one egg mass is developed, but if rows are viewed, the strongly convex side of one capsule follows the weakly convex side of the next. The basal membranes of neighboring capsules in an egg mass are usually fused together with their rims. Each peduncle of the vasiiform capsules is solid and round in cross section, and fixed to it laterally displaced. Symmetry of the capsules is bilateral with one slightly concave or convex side and another strongly convex side, separated from each other by a narrow ridge which can be traced onto the basal membrane. Each capsule consists of 2 well differentiated layers, the outer one smooth, colorless and transparent, and the inner one radially striped, opaque. The outer wall is fused with the peduncle and the basal membrane, and shows one larger and one smaller protrusion on each side of the narrow apical plate. The inner wall is more rounded, extends only a short way into the apical protrusions and not at all into the foot. The apical plate is narrow and of oval shape, and completely taken up by the escape aperture. Where the inner and outer walls fuse, a ridge is formed, surrounding the clearly transparent membrane that closes the escape aperture. This membrane

dissolves after about 18 days when the embryos are ready to hatch. All 9 - 21 embryos hatch as crawling young. The dimensions of the capsule are: 6mm high, $3\frac{1}{2}$ mm wide, $2\frac{1}{2}$ mm thick. Eggs are yellowish white at first and the hatching embryos are white.

Conus largillierti Kiener, 1848

(Figures 11A, 11B)

Spawn of *Conus largillierti* has been dredged up from soft bottom in the NW-part of the Gulf of Uraba between Isla Napu and Terron de Azucar by Rudo von Cosel. The eggs had been deposited on the shells of dead bivalves. A freshly caught female deposited 3 capsules on the wall of an aquarium on 13 April 1971. A female held for some time in an aquarium by von Cosel attached an egg mass

of 44 capsules on 26 April 1971. This egg mass consisted of 4 layers, and the lowest layer was attached to the underside of a rock forming the roof of a small cave in the aquarium.

Each capsule is attached to the substrate or the underlying capsule by a basal membrane. The rims of these membranes in neighboring capsules of one row are fused to each other. In each row the capsules are arranged in such a way that all escape apertures point in the same direction. Within one egg mass, all rows are directed the same way as well as those attached on top of them.

The shape of each capsule of *Conus largillierti* is very similar to that described by D'ASARO (1970a) for *C. spurius atlanticus* Clench, 1942. Each flattened, tongue-shaped capsule has a wrinkled and a smooth side. The whole capsule stands on the substrate inclined, the smooth side closer to the substrate than the wrinkled side. The wrinkles

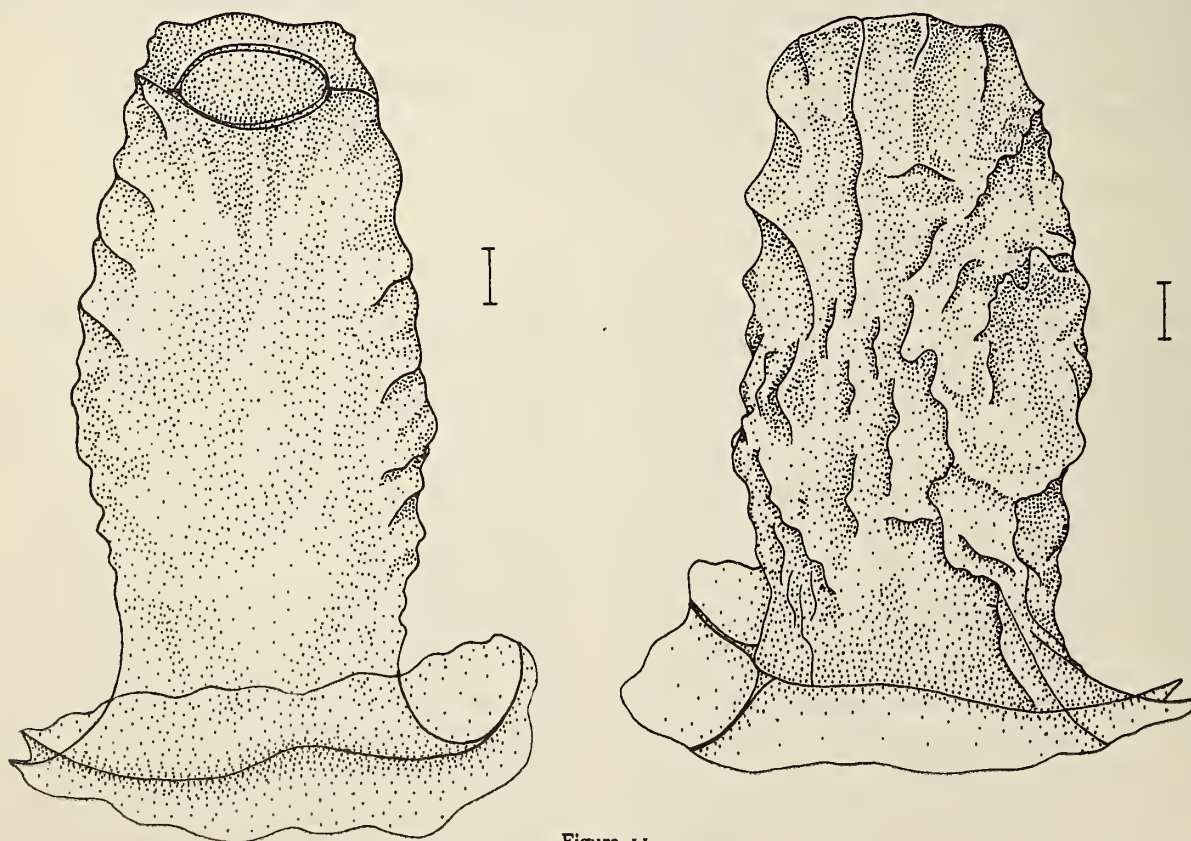


Figure 11

Egg capsule of *Conus largillierti*

A. seen with its concave side

B. seen with its convex side

(scale = 1 mm)

show a vertical direction but are, if viewed in detail, rather irregular in their course. The apical region has a large oval escape aperture which is closed by a transparent membrane, while the remainder of the capsule is opaque white. All apical plates are tilted toward the smooth side. A suture dividing the capsule into 2 unequal halves follows the narrow sides of the capsule, is only faintly visible and crosses the membrane of the escape aperture along its longest axis. After more than 10 days of development, all 20 to 40 embryos contained within one capsule hatch through the dissolved escape aperture membrane as veliconcha, being able to crawl and to swim. Capsule dimensions are: up to 7 mm wide, up to 12 mm high, and about $1\frac{1}{2}$ mm thick.

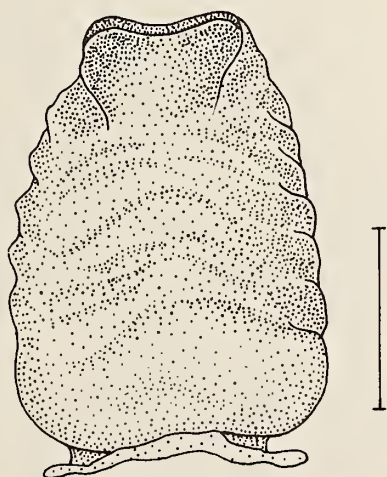
Conus ermineus Born, 1778

(Figures 12A, 12B)

Spawn of *Conus ermineus* was attached to the underside of living hemispherical coral colonies in the shelter of the coral reef of Chengue bay. Here the capsules of *C. regius* are also found, though much more commonly than those of *C. ermineus*. Spawning females were collected as they were in the act of secreting their spawn. Egg cases of this species were also found near the Carmabi in Curaçao, at-

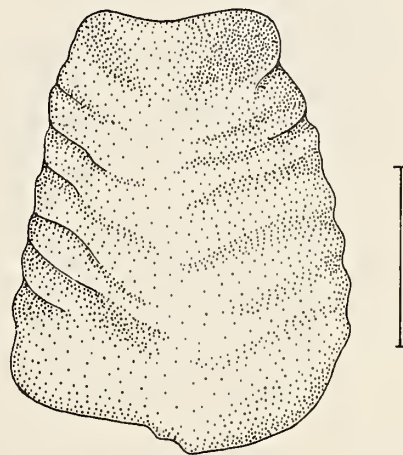
Figure 12

Egg capsule of *Conus ermineus*
(scale = 1 cm)



A. seen with its concave side

tached to the lower side of living and dead stone corals. The general shape of the capsules is very similar to that of *C. regius*. Capsules are arranged in rows. Each capsule is attached, somewhat inclined, to a basal membrane. The edges of these membranes are fused to each other within the rows of capsules.



B. seen with its convex side

The flattened, roughly rectangular, opaque white capsules are wider at the base than near the top. The side of the capsules furthest away from the substrate is transversely wrinkled. The wrinkles continue into undulations on the narrow capsule sides and disappear near the edge of the capsule closest to the substrate. The escape aperture occupies the entire narrow apical region and is closed by a clear, transparent membrane. A curved ridge extends down the smooth capsule side from each narrow end of the escape aperture.

About 500 white eggs will all develop into veligers which hatch after more than 10 days. Average dimensions of the capsules are: 20 mm high, 14 mm wide, and $1\frac{1}{2}$ mm thick.

Terebra cinerea (Born, 1778)

(Figures 13A, 13B)

Animals kept in the aquarium produced some egg capsules right after they had been collected in the bay of Naguan-ge. These capsules were attached to the shells of a bivalve of the genus *Isognomon*.

The egg mass shows no pattern; each capsule is cupola-shaped. The basal membrane, which fixes the capsule to the substrate, extends into a broad rim much beyond the

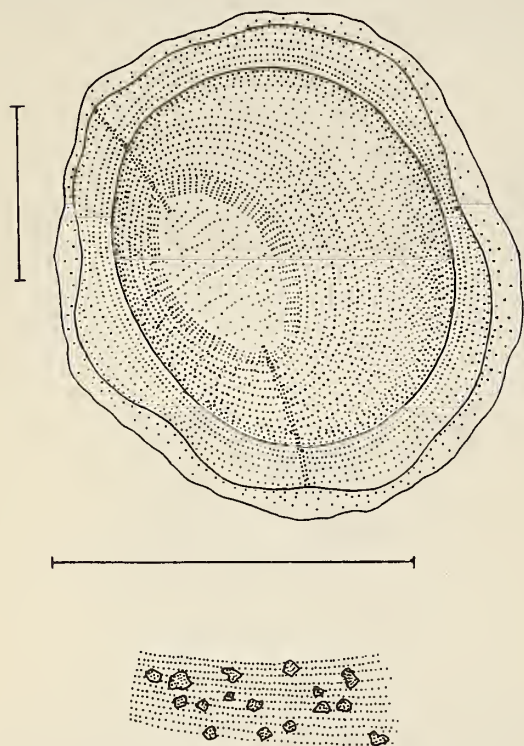


Figure 13

Egg capsule of *Terebra cinerea*

A. seen from above

B. detail of the rim

(scale = 1 mm)

capsule walls and has very fine concentric lines. Sand grains may be incorporated into the surface of the basal membrane at the edges of the rim. The escape aperture is large, extending from the basal part of the cupola almost to its top. A suture, invisible on the membrane which closes the escape aperture, but well visible from the end of the oval aperture down to the basal membrane, divides the capsule into 2 unequal parts. The cupola, besides wart-like granules, possesses fine lines following the general shape of the escape aperture. The latter is surrounded by a thickened ribbon with transverse ridges. Very fine transverse lines may also be noted on the clear, colorless membrane of the escape aperture.

The slightly opaque capsules measure 3.2 mm in length, 3.0 mm in width and 1 mm in height. Each capsule contains 2 embryos, which hatch after 30 days development as crawling young.

Drillia solida C. B. Adams, 1830

(Figure 14)

Animals kept in the aquarium produced spawn, consisting of a few cupola-shaped capsules in January and June, 1971. These capsules were attached without any definite pattern to the wall of the aquarium.

The capsules were attached by a large basal membrane extending beyond the cupola in a wide, irregularly bordered rim. The cupola is low and evenly formed with a central round to slightly oval escape aperture. The cap-

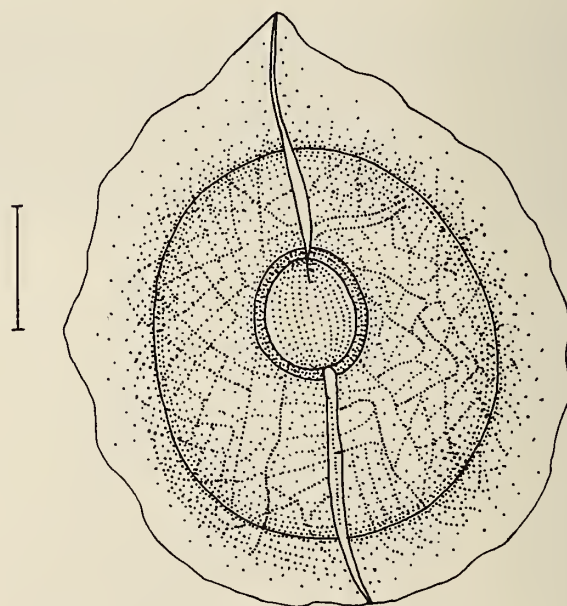


Figure 14

Egg capsule of *Clathrodrillia solida* seen from above
(scale = 1 mm)

sule is differentiated into 2 equal halves by a suture that indistinctly crosses the membrane which closes the escape aperture; the suture extends into the rim of the basal membrane as a strong ridge on the capsule walls. The cupola is sculptured by a number of irregularly dispersed wrinkles crossing each other. They extend halfway onto

the rim of the basal membrane and end in the ridge surrounding the escape aperture. This ridge has concentric lines. The colorless membrane of the escape aperture also has concentric lines which produce a pattern resembling a cut onion. Aside from this and the basal membrane, which are colorless and transparent, the walls of the capsule are opaque.

Each capsule has an almost round outline, is about 4 mm wide and 1 mm high. All 2 - 7 whitish embryos develop in 14 days into light brown veligers.

Crassispira sp.

(Figure 15)

Where individuals of *Crassispira* sp. were commonly found, as for example just offshore in the bay of Taganga, wood fragments, small pebbles and living and dead mollusk shells often were covered with cupola-shaped capsules. Hard substrates are rare in the normal living-environment of this species so that the few found are frequently used to attach the spawn. The basal membrane extends into a rim with a fine concentric wrinkle-sculpture on it. The shallow cupola has an escape aperture closed by a clear, colorless membrane in its center. The escape aperture is surrounded by a ridge with transverse lines as seen on capsules of *Terebra cinerea*. A suture crossing the cupola and the membrane of the escape aperture divides the capsule into 2 not quite equal halves. The whitish, opaque walls are delicately wrinkled by numerous small wrinkles very much like a finger print without concentric or radial

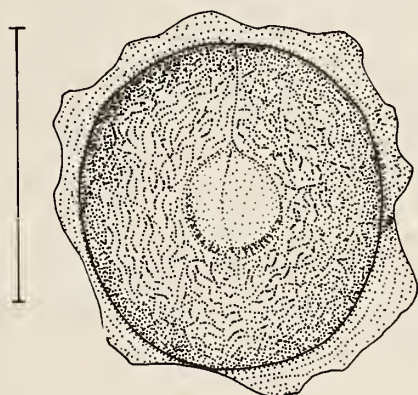


Figure 15

Egg capsule of *Crassispira* sp. seen from above
(scale = 1 mm)

pattern. Only near the outer rim is found a more concentric arrangement.

Each capsule is about 1½ mm wide, somewhat oval in outline, and quite low. Two to 5 eggs develop and hatch as crawling young.

DISCUSSION

Among the 13 species of higher Neogastropoda described here, 4 groups of capsule morphologies can be distinguished, some of which show close relation to groups differentiated within the Muricea and Buccinacea (BANDEL, 1975a, 1975b, in press), while others are quite distinct.

1. Group of *Oliva reticularis*

The egg mass of *Oliva reticularis* is quite different from any prosobranch egg mass so far known. No other species known produces a tube consisting of flat, scale-like capsules attached to each other from the inside of it. The egg mass can therefore be buried within the substrate, like the female that produces the egg mass, as long as the inner cavity of the tube remains open to seawater. The escape apertures of all capsules point toward the inside of the tube so that the hatching veligers can leave the egg mass through the inner cavity of the tube. Females were not observed guarding the egg tube, but capsule production by a female seems to be very slow. Therefore, the oldest capsules near the closed end of the tube are already well developed when the youngest capsules are deposited near the rim of the tube aperture. This rim extends above the surface of the sediment when the female leaves the spawn after the end of secretion. It does not guard the spawn as described by BANDEL (1975d, in press), D'ASARO (1969), and HOWARD (1962) for different members of the Tonacaea.

The closely related *Oliva sayana* Ravenel, 1834, kept in the aquarium in Florida produced spherical egg capsules with 14 to 48 eggs each, released singly and unattached on the surface of the sand (D'ASARO, 1970a; OLSSON & CROVO, 1968).

Regarding the shape of a single capsule within an egg mass, the group of *Oliva reticulata* shows great similarities to the group of *Terebra cinerea* (below) or the groups of *Colubraria swifti* (Tryon, 1881) (BANDEL, 1975a, in press) or *Drupa nodulosa* C. B. Adams, 1845 (BANDEL, 1975b, in press), characterized by shallow, cupola-shaped capsules that are attached by a wide basal membrane with its entire lower surface to a hard substrate, contrasting with *O. reticularis*.

2. Group of *Olivella perplexa*

The capsules of the group of *Olivella perplexa* are characterized by hemispherical egg cases attached to the substrate by a basal membrane, round in outline. The cupola is differentiated into an upper lid and the lower capsule walls. At time of hatching the lid falls off as a whole, dissolved from the remaining capsule wall by a thin separating line. This differentiates this group from that of *Terebra cinerea* (below), where the membrane of the escape aperture does not fall off, but is dissolved. Similar escape aperture membranes are found in egg capsules within other prosobranch groups, i. e., the Neritacea in general (ANDREWS, 1935; KNUDSEN, 1950; LEBOUR, 1945; THORSON, 1946; own observations) or *Anachis obesa* (C. B. Adams, 1845) (BANDEL, 1974a).

In *Olivella perplexa* the upper lid is situated on top of well developed capsule sides and makes up only the apical region of a capsule cupola. Similar capsules are produced by *O. pusilla* (Marrat, 1871) (PERRY & SCHWENGEL, 1955) and *O. mutica* (Say, 1822) (PAINE, 1962). *Marginella marginata* Born (KNUDSEN, 1950), *M. eveleighi* Tomlin & Shackelford, 1913 (KNUDSEN, *op. cit.*), *M. everyi* Petit (KNUDSEN, *op. cit.*) and *Persicula persicula* (Linnaeus, 1758) (KNUDSEN, *op. cit.*) also produce capsules of this general appearance.

Other capsules of this group carry the line separating the lid from the side walls at the middle of the cupola. Here can be listed the sculptured capsules of *Olivella verreauxii* (Duclos, 1857) (MARCUS & MARCUS, 1955) and the smooth ones of *O. fulgurata* (A. Adams & Reeve), (AMIO, 1963).

Lid rims situated close to the base of the cupola, leaving almost no walls beside the lid attached to the basal membrane, are found in *Hyalina avena*, *Olivella biplicata* (Sowerby, 1825) (EDWARDS, 1968), *Microvoluta marginata* (Hutton, 1885) (PONDER, 1972), *Marginella adamsonii* Kiener (KNUDSEN, 1950), and *Prunum apicinum* Menke, 1828 (D'ASARO, 1970a).

All of these capsules, excepting those of *Hyalina avena*, contain one egg each and most young hatch after metamorphosis is completed, as crawling young, a few during metamorphosis as veliconcha (*Olivella verreauxii*, *O. biplicata*).

3. Group of *Terebra cinerea*

Capsules of the group of *Terebra cinerea* are attached to the substrate by a round basal membrane. On it rises a shallow cupola with an oval centric or excentric escape aperture closed by a membrane that dissolves before the young hatch. Within the Meso- and Neogastropoda this type of capsule is quite common, as, for example, in the

Rissoidae (FRETTER, 1948; FRETTER & GRAHAM, 1962; LEBOUR, 1934, 1936, 1937; THORSON, 1946), in the Muricacea (AMIO, 1963; BANDEL, 1975b, in press; LEBOUR, 1936; THORSON, 1940, 1946), in the Buccinacea (AMIO, 1957, 1963; BANDEL, 1974, 1975a, in press; COWAN, 1965; FIORONI & PORTMANN, 1968; MARCUS & MARCUS, 1962; THORSON, 1935, 1940) and in the group of higher Neogastropoda discussed here.

The simplest form is found in *Vexillum puella* with smooth capsules showing only the central oval escape aperture after its membrane has been dissolved just before the hatching of the young. *Mitra ebenus* Lamarck (FRANC, 1942) produces capsules quite similar in shape to those of *Vexillum puella*, but here the escape aperture is well visible before hatching.

The capsules of *Voluta virescens* are large and have a distinct escape aperture in an excentric position. *Voluta musica* Linnaeus, 1758 (LAMY, 1928; CLENCH & TURNER, 1970) has the same type of capsule as well as *Narica cancellata* Chemnitz (RISBEC, 1935). But in contrast to the former, the latter contains many eggs which all hatch as veligers, while in *Voluta* only a few animals hatch, eating during their development all of the numerous eggs originally present.

Terebra cinerea and *Drillia solida* have watch-glass-like capsules with ornamentation on the walls and a sculptured escape membrane. While this membrane is excentrically situated in *Terebra*, it is centrally located in *Drillia* and *Crassispira*. This last type of capsule is rather commonly found in the Turridae. Such capsules with ornamentation of the walls are secreted by *Philbertia purpurea* Montagu (FRANC, 1950), *P. gracilis* Montagu (FIORONI, 1966; FRETTER & GRAHAM, 1962; LEBOUR, 1933, 1934). Capsules with smooth walls are produced by *Bela trevelyana* Turton (THORSON, 1946), *B. turricula* Montagu (VESTERGAARD, 1935), *Clavus japonicus* Lischke, (AMIO, 1963), *Drillia crenularis* Lamarck (THORSON, *op. cit.*), *Mangelia nebula* Montagu (LEBOUR, 1934, 1937) and *Philbertia linearis* Montagu (THORSON, *op. cit.*).

Even though the shape of egg capsules within the Turridae is the same, the sculpture of the walls shows many different patterns. As recent studies of my own on additional capsule material of this group from the Mediterranean Sea have shown, most species can be differentiated from each other by the sculpture and size of the egg capsule alone.

4. Group of *Conus regius*

Members of the genus *Conus* produce egg capsules that are very much alike in shape and in the general pattern of the egg mass. All capsules have a flattened shape, stand

on a short peduncle and possess apical oval or slitlike escape apertures.

Conus jaspideus pygmaeus has rounded and very smooth capsular shapes. The capsules of *C. jaspideus* Gmelin, 1791 were described by PERRY & SCHWENGEL, 1955 from Florida in very general terms. They seem to be similar to *C. jaspideus pygmaeus*. Smooth capsules are described for *C. vayssetianus* Crosse (PETIT & RISBEC, 1929). All other capsules have wrinkled sides quite similar to *C. regius*, *C. mus*, *C. ermineus* and *C. largillierti*. LEBOUR (1945) figured capsules of *C. mus* from Bermuda, but description and drawing (textfigure 31) can only place these capsules within the general *Conus* morphology.

It seems as if most species of this genus produce capsules that can be differentiated from those of other species. Capsular morphology, therefore, could be of value in the difficult task to differentiate true *Conus* species from ecological and geographical races.

Descriptions of *Conus* spawn of different species were published by AMIO, 1963; D'ASARO, 1970a, 1970b; FRANC, 1942; KNUDSEN, 1950; KOHN, 1961a, 1961b; WOLFSON, 1969. A difference may also be noted in the shape of the whole egg mass as D'ASARO (1970a) reported. My own studies on *Conus mediterraneus* Hwass, 1792, from the Mediterranean Sea have shown that the form of the egg mass of this species depends very much on the age and size of the female producing it as well as on the size and consistency of the place of attachment. If the female is small, the size of the capsule is also small and one egg mass consists of few capsules. If the female is large, larger and more numerous capsules are the result. If the place for attachment of spawn is a narrow, restricted cavity under a rock, the egg mass may consist of more than one layer of capsules, one on top of the other. The same is the case if many females crowd into a large cavity, all secreting capsules at the same time. If large space for attachment is available and only one or a few females produce spawn at a time, egg masses are attached in loosely distributed, long, continuous rows in a single layer, not on top of each other.

In addition to the 4 groups of capsule morphologies in the higher Neogastropoda discussed here, 4 additional groups could be differentiated based on the egg masses described in the literature. One could be grouped around a number of species of the genus *Mitra* with vasiform capsules (CATE, 1968; CERNOHORSKY, 1970; D'ASARO, 1970a; LAMY, 1928; OSTERGAARD, 1950; WOLFSON, 1969), a second around the spawn of *Harpa* with peculiar rows of flattened capsules (RISBEC, 1932), a third around *Austromitra* with capsules secreted into the outer epidermis of tunicates (PONDER, 1972) and a fourth with

Melo secreting honey-combed, glassy, cylindrical egg masses (AMIO, 1963; HORNEILL, 1921; LAMY, 1928).

DESCRIPTION OF *Crassispira* sp.

Shell: Height up to 23 mm, width up to 7 mm; total of 10 whorls; protoconch $1\frac{1}{4}$ whorls. Embryonic shell figured and described by BANDEL (1975c: plt. 21, fig. 8; p. 86). At hatching translucent, later white shell with no sculpture except strong growth-lines. Aperture smooth, twice as

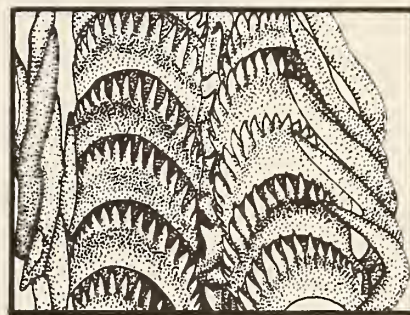


Figure 16

Section of the radula of *Crassispira* sp. redrawn from a scanning-electron micrograph (scale = 0.1 mm)

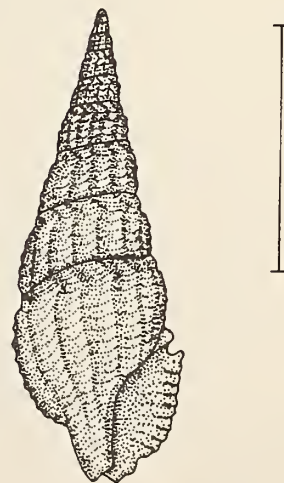


Figure 17

Shell of *Crassispira* sp.
(scale = 1 cm)

high as wide. Embryonic shell 0.65 mm high. Junction of protoconch to teleoconch distinct. Adult shell solid, fusiform, white, pinkish-white, or dirty white in color. Anterior end short, truncated. Sculpture with a broad subsutural fold. Sinus moderately deep, U-shaped. Outer lip of adult individuals somewhat extended outwardly, with 6 - 8 shallow denticles or ridges on its inner side. Thirteen to 16 axial ribs crossed by 17 - 20 spirally arranged threads on the last whorls. Ribs somewhat oblique to the long axis of the shell, extending onto the subsutural cord. Operculum small, dark dirty brown to almost black.

Soft parts: Visible soft parts show a general opaque white coloration with numerous white spots of non-opaque pigment. On the side and base of the foot, as well as the base of the tentacles and the siphon, round red-brown pigment spots loosely distributed are found. Eyes large, tentacles short, siphon long.

Radula: 0.2 mm wide with 5 teeth in each row. Central tooth small, thorn-like with one central cusp. Lateral tooth crescentic with smooth, concave base, and blade with 17 - 19 denticles. All denticles of the lateral teeth narrow and pointed, central ones largest. Marginal teeth arrow-shaped, similar to teeth of *Conus*. In general outline bent like a sickle and of equal width from base to tip. Narrowly pointed and hooked at the top.

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ERRATA

In the paper by K. BANDEL, *The Veliger* vol. 18 on "Observations on spawn, embryonic development, and ecology of some Caribbean lower Mesogastropoda" a species name was spelled in three different ways. On page 249 the name appears as *Cingula babylonia* and in the explanation to figure 18 on page 263 as *Cingulum babylonia*. The correct name is *Cingulina babylonia*. The editor apologizes for having overlooked these discrepancies and the author apologizes for not having seen these errors in the manuscript and in the proofs.

